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The importance of behaviour in improving the production of shrimp in aquaculture

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ABSTRACT

There is increasing recognition within the aquaculture industry that understanding the behaviour of farmed animals can help provide solutions to feeding problems. However, most studies have focused on finfish production, with fewer behavioural studies on feeding processes in commercially-produced crustaceans. More than 60% of crustacean aquaculture is attributed to the production of penaeids, particularly the Pacific white-leg shrimp (*Litopenaeus vannamei* Boone). The profitability of the Pacific white-leg shrimp for aquaculture stems from its ability to survive in a wide range of environments and its fast growth at high densities. However, there are significant setbacks within their farming. In particular, while they can move rapidly to take food pellets, they can be slow to consume them leading to food wastage and subsequent economic losses for the industry. Understanding shrimp behaviour provides a starting point for refinements to feeding practices. Here we review the different influences on shrimp behaviour which are likely to influence productivity such as individual-level effects (e.g. moulting, sex), environmental influences (e.g. photoperiod, conspecific presence) and water quality (e.g. salinity, temperature). Although work on feed management has been conducted, providing information on nutrition, feeding frequency and schedules, here we demonstrate that such advances must be accompanied by behavioural approaches to allow development of optimal feeding efficiencies and to support the continued growth of the crustacean aquaculture industry.

Key words: Aquaculture, Chemoattraction, Crustacean, Feeding behaviour, Feeding effectors, *Litopenaeus vannamei*.

INTRODUCTION

The production of crustaceans in aquaculture is a global industry with large commercial and economic importance (Bondad-Reantaso *et al*. 2012). Marine shrimp in particular dominate crustacean aquaculture (Briggs *et al*. 2004) and of the 7 million tonnes produced annually, more than 60% is attributed to the production of penaeid shrimp (FAO 2016). Many countries rely heavily on such shrimp production and as a result it has been one of the fastest growing aquaculture sectors in Asia and America (Briggs *et al*. 2004; Funge-Smith & Briggs 2005; FAO 2016).

Modern day shrimp aquaculture originated in Japan in the 1930s (Rosenberry 2001; Chamberlain 2010), however technologies developed in the 1970s expanded production in other Asian countries, such as Indonesia, the Philippines and Thailand as well as the Americas (Rosenberry 2001; Chamberlain 2010; Nash 2011). Initially the main focus of this development was the culture of the tiger shrimp (*Penaeus monodon* Fabricius) (Yi *et al*. 2016), for which there was a large demand in Asian and US markets (Nash 2011; Rimmer *et al*. 2013). However, the intensification and densification of *P. monodon* farming led to outbreaks of disease in the 1990s that severely depleted aquaculture stocks over a decade (Flegel 2009). As a result, the culture of Pacific white-leg shrimp (*Litopenaeus vannamei* Boone) was introduced (Hall 2004; Flegel 2009; Chamberlain 2010), and it is now the most heavily farmed shrimp species representing around 80% of total marine penaeid shrimp production (FIGIS 2015).

The focus on *L. vannamei* production was partly due to advantages over *P. monodon* with regards to disease resistance (Liao & Chien 2011; Bondad-Reantaso *et al*. 2012).

Additionally, the species has an increased tolerance to high stocking densities (typically 60-150/m^2, but up to 400/m^2) (Briggs *et al*. 2004; Funge-Smith & Briggs 2005; Jory & Cabrera 2012), improved feed conversion rates and low protein requirements (of around 20-35% crude protein) (Briggs *et al*. 2004; Funge-Smith & Briggs 2005; Bondad-Reantaso *et al*. 2012; Jory & Cabrera 2012), higher average daily growth rates (up to 3 g/week) (Briggs *et al*. 2004; Funge-Smith & Briggs 2005; Bondad-Reantaso *et al*. 2012; Jory & Cabrera 2012), high tolerance to a large range of water parameters including salinity and temperature (Briggs *et al*. 2004; Funge-Smith & Briggs 2005; Bondad-Reantaso *et al*. 2012; Jory & Cabrera 2012), and higher survival rates during larval rearing (50 – 60%) (Funge-Smith & Briggs 2005). Moreover, in marketing terms, *L. vannamei* has been shown to be preferred by consumers over *P. monodon* (Funge-Smith & Briggs 2005).

As a result of this intensification of production, *L. vannamei* has been the subject of a large number of scientific studies that has resulted in substantial knowledge on the biology (e.g. Chamberlain & Lawrence 1981; Dall *et al*. 1990; Vega-Villasante *et al*. 2000), genetics (e.g. Garcia *et al*. 1994; Gitterle *et al*. 2005) and zootechnics (e.g. Briggs *et al*. 2004; Cuéllar-Anjel *et al*. 2010) of the species. Feeding efficiency of farmed stock has been an important focus, however there is a general lack in information of individual feeding behaviour and the aspects that may be important for determining optimal feeding efficiency in *L. vannamei*, as well as in other commercially important species. This paper therefore, with a specific focus on *L. vannamei*, reviews the current problems associated with the feeding of farmed shrimp and how understanding their behaviours may promote greater feeding efficiency and subsequent increases in production. By drawing on behavioural information from neurophysiological and nutritional studies which have been developed in *L. vannamei* as well as other commercial and non-commercial crustacean species, we aim to present

considerations that we believe to be important for detecting and developing optimal feeding practices.

FEEDING PROBLEMS IN SHRIMP AQUACULTURE

Crustacean aquaculture continues to experience global growth (Bondad-Reantaso *et al*. 2012). However, there are a range of factors that contribute to inefficiencies in farming practices leading to reduced production as well as significant economic losses (Neiland *et al*. 2001; Engle *et al*. 2017). Common problems include poor larvae production across a range of farmed species (Juinio-Menez & Gotanco 2004; Thuy & Ngoc 2004; Vijayakumaran *et al*. 2009; Jeffs 2010), the incidence of disease (Rodríguez *et al*. 2003; Flegel 2009), pollution effects due to waste products (Briggs & Funge-Smith 1994; Martin *et al*. 1998; Boyd *et al*. 2007), and the escape of individuals (Cuéllar-Anjel *et al*. 2010; Felix 2013). Of particular interest here, however, are the studies that have documented the feeding inefficiencies associated with crustacean production (e.g. Chanratchakool *et al*. 1998; Davis *et al*. 2006; Boyd *et al*. 2007; Smith & Tabrett 2013), which are predominantly in relation to expensive feed production costs, feeding-management practices as well as poor feeding efficiency by individuals.

The manufacture of feed is one of the largest costs in aquaculture production (Lawrence & Lee 1997; Boyd *et al*. 2007; Smith & Tabrett 2013; Zhou *et al*. 2017), and depending on the system in question, may represent as much as 60-80% of total production costs (Chanratchakool *et al*. 1998; Hertrampf & Piedad-Pascual 2000; Smith *et al*. 2002; Cuzon *et al*. 2004; Rola & Hasan 2007; Hasan & New 2013). Commercial shrimp feed formulations

commonly include fish meal, often representing the primary and most expensive protein ingredient (Lim & Dominy 1990; Tacon & Barg 1998; Dersjant-Li 2002; Cruz-Suárez *et al*. 2007). There are clear beneficial effects of marine protein sources for crustacean nutrition, such as the presence of essential fatty acids, vitamins, cholesterol and minerals, in addition to the enhancement of feeding activity, palatability and growing processes through attractants and growth factors (Molina-Poveda *et al*. 2002; Cruz-Suárez *et al*. 2007; Sookying *et al*. 2013). However, the current state of global fish stocks has triggered a costlier production of fish meal (Hardy & Tacon 2002; Sookying *et al*. 2013), and as a result, less expensive plant and terrestrial animal proteins are being increasingly used in aqua-feed formulations since they are readily available, economical, and sustainable (Lim & Dominy 1990; Watanabe 2002; Samocha *et al*. 2004a; Amaya *et al*. 2007; Gatlin *et al*. 2007; Naylor *et al*. 2009; Sookying *et al*. 2013). Moreover, studies specifically on *L. vannamei* suggest that it is possible to replace around 75-100% of the total amount of crude protein with proteins of non-marine origin, without compromising shrimp performance (Davis & Arnold 2000; Fox *et al*. 2004; Hernández *et al*. 2004; Samocha *et al*. 2004a; Amaya *et al*. 2007).

A major restriction in shrimp aquaculture is often an inability to observe stock during its development, causing difficulties for determining biomass and survival (Davis *et al*. 2006; Smith & Tabrett 2013). Feed management is therefore a complex task during shrimp production, often resulting in overfeeding and the generation of large amounts of waste (Martinez-Cordova *et al*. 1998; Nunes & Parsons 1999; Davis *et al*. 2006; Sun *et al*. 2016). Overfeeding can lead to high levels of non-beneficial microorganisms in addition to hypoxic conditions at certain times within the day, therefore shrimp feeding protocols must be well organised in time as well as space and in accordance with population size (Cuéllar-Anjel *et al*. 2010). In addition, feed waste may be compounded by poor physical quality of feed and/or

environmental conditions (see environmental and water quality effects sections), which negatively influence crustacean sensorial capacity and food detection. Poor physical quality of feed can lead to premature breakdown of food (Davis *et al*. 2006) and reduce food digestibility through nutrient leaching (Sanchez *et al*. 2005; Cruz-Suárez *et al*. 2007). Spoilage of food combined with poor environmental conditions could also result in oversaturation of chemoreceptors (Lee & Meyers 1996; De la Haye *et al*. 2012), and disruption of chemical cues within the water (Lee & Meyers 1996; Nunes *et al*. 2006). Studies exist on the relationships between shrimp species, stock mass and size, and the correct amount of feed required for optimal production (Jory 1995; Jory & Cabrera 2012). However, the difficulties in checking development of the whole stock can make dispensing the optimal quantity of feed difficult. The use of feeding trays or automatic feeders in shrimp farming is one solution to this problem as they are useful for the control and monitoring of the amount of feed consumed by shrimp, and thus reduce the incidence of overfeeding (Martinez-Cordova *et al*. 1998; Bador 2000; Pontes & Arruda 2005b; Molina & Espinoza 2018). In addition, automatic feed dispensers using passive acoustic systems (hydrophones) can measure the quantity of feed consumed by shrimp which provides a more accurate estimate of the current feeding demand in ponds when compared to feeding trays (Smith & Tabrett 2013). This in turn can improve the environmental conditions of the production ponds (Seiffert & Andreatta 2004; Cuéllar-Anjer *et al*. 2010). However, for this to be a truly effective solution there needs to be high feeding efficiency of individuals, which can be confirmed by the collection of behavioural data (Zhou *et al*. 2017).

CRUSTACEAN FEEDING BEHAVIOUR

185 We suggest here that in order to address the problems associated with feeding efficiencies, a
186 focus on individual feeding behaviours in crustaceans is necessary. Therefore, an important
187 step is to outline the mechanisms involved in food detection and to link shrimp physiology to
188 behaviour. Crustaceans are considered to be generalist feeders (Smith *et al*. 2005; Hay 2011).
189 They must identify chemical cues of potential food, distinguishing relevant cues against
190 background chemicals and determining their qualities (i.e., molecular structures), quantities
191 (i.e., concentrations), and locations (i.e., spatiotemporal dynamics) (Lee & Meyers 1996;
192 Moore & Grills 1999; Derby *et al*. 2001). They respond to primary metabolites (e.g. sugars,
193 proteins, amino acids, products of respiration, metabolic wastes) because these indicate the
194 presence of food resources in general (Carr 1978; Zimmer-Faust 1987; Hay 2011).
195
196 In the case of decapod crustaceans, such as *L. vannamei*, there are three different detection
197 paths for locating a food source that include the visual, mechanoreceptor and chemoreceptor
198 systems, with associated receptors which are present on most shrimp appendages. However,
199 decapods perceive food mainly via chemical stimuli rather than mechanoreception or vision
200 as water is an excellent medium to transmit these types of cues (Hindley 1975; Atema 1995;
201 You *et al*. 2006). Crustaceans use chemoreception to intercept food across longer distances
202 and once in closer proximity to the food source they can apply visual and mechanoreception
203 detection. As such, these two pathways of detection act to obtain additional information in
204 relation to feeding processes (Derby & Sorensen 2008).
205
206 **Chemosensory receptors**
207 Crustaceans possess a large number of chemoreceptors that are packaged into sensilla that are
208 simple sensory receptors consisting of modified hair-shaped cells (Derby & Sorensen 2008).
209 Sensilla are extremely diverse in structure and are distributed over the body on antennules,

but also on the second antennae, legs, mouthparts, cephalothorax, abdomen and telson (Gleeson *et al*. 1993; Cate & Derby 2001; Horner *et al*. 2004; Derby & Sorensen 2008). This wide distribution allows crustaceans to maximise their ability to locate and discriminate environmental chemical cues and physical information (Steullet *et al*. 1999; Horner *et al*. 2000; Derby & Steullet 2001).

Each antennule has hundreds of thousands of chemoreceptor neurons (Grünert & Ache 1988; Cate & Derby 2001) and is sensitive to many different chemicals, in particular small, water-soluble molecules such as amino acids, amines, nucleotides, and sometimes sugars and peptides (Ache 1982; Carr *et al*. 1984; Carr & Derby 1986). Antennular chemoreception is specialized for detection of chemical cues (Rittschof 1992; Koehl 2011) and plays an important role in search initiation and orientation toward the source of a distant chemical stimulus (Reeder & Ache 1980; Devine & Atema 1982; Derby 2000; Derby *et al*. 2001). The majority of chemoreceptors are found on the non-aesthetasc/non-olfactory regions on the medial and lateral flagella of the antennules (Schmidt *et al.* 1992; Cate & Derby 2001; Steullet *et al*. 2002; Horner *et al*. 2004; Schmidt & Derby 2005). In addition, crustaceans possess a tuft on the distal part of the lateral antennular flagella which is composed of chemoreceptor sensilla, denominated as the aesthetasc/olfactory region (Grünert & Ache 1988; Derby *et al*. 2001; Steullet *et al*. 2002; Horner *et al*. 2004), and is the most intensively studied part of crustacean chemosensory pathways (Grasso & Basil 2002; Derby & Sorensen 2008). Studies have demonstrated that aesthetasc and non-aesthetasc regions have some functional redundancy. For example, work with spiny lobster (*Panulirus argus* Latreille) (Reeder & Ache 1980; Derby *et al*. 2001; Steullet *et al*. 2001; Schmidt & Derby 2005), American lobster (*Homarus americanus* H. Milne-Edwards) (Devine & Atema 1982) and crayfish (*Cambarus bartonii* Fabricius) (Dunham *et al*. 1997) has revealed that after selective

235 removal of their aesthetasc sensilla, these animals can compensate for the loss if their non-
236 aesthetasc chemoreceptors are intact. Therefore, both kinds of receptors assess the quality of
237 food, mediate olfactory learning and enable orientation to distant food sources (Derby *et al*.
238 2001; Steullet *et al*. 2001, 2002: Horner *et al*. 2004).
239
240 Chemical receptors located on other parts of the body are also important. Pereopod dactyl
241 chemoreceptors control local grasping reflexes and food recognition (Fuzessery & Childress
242 1975; Zimmer-Faust & Case 1983; Dunham *et al*. 1997). Walking legs may play a leading
243 role in food detection if the crustacean has lost the antennules (Hazlett 1971). Maxillipeds
244 and mouthpart chemoreceptors mediate the decision to ingest food (Derby & Atema 1982;
245 Derby *et al*. 2001; Aggio *et al*. 2012), whereas pleopod beating produces a water current
246 around the shrimp carrying organic molecules. This activity may provide additional
247 information via chemoreception on the presence of prey, conspecifics or predators (Devine &
248 Atema 1982; Costero & Meyers 1993; Atema 1995; Klages *et al*. 2002), however, the precise
249 role of these chemoreceptors on the parts of the body detailed here is poorly understood.
250
251 In addition to all chemical receptors which mediate food recognition and ingestion, a recent
252 study has identified a novel pathway of branchial nutrient absorption in the green shore crab
253 (*Carcinus maenas* Linnaeus). This phenomena is the first finding in marine arthropods
254 (Blewett & Goss 2017) and may provide a new level of complexity to crustacean nutrition.
255
256 **Behavioural responses**
257 Chemosensory stimuli mediate all phases of feeding in crustaceans (Holland & Borski 1993;
258 Grey *et al*. 2009), and these can be categorised into a series of behavioural responses such as
259 detection and orientation towards a food source (Ache 1982; Kurmaly *et al*. 1990; Lee &

Meyers 1996; Moore & Grills 1999) and handling of food (Steiner & Harpaz 1987; Lee & Meyers 1996; Derby *et al*. 2016). In general, when feed is offered, crustaceans change their behavioural profile and there are observed increases in the frequency of behaviours related to searching for feed, such as exploration and crawling, and feed grabbing (Da Costa *et al*. 2016). This is coupled with a decrease in the frequency of those behaviours not associated with feeding, such as cleaning and burying (Pontes & Arruda 2005a; Silva *et al*. 2012). Crustaceans have also been noted to express habituation behaviours, including learning to search in a particular area or type of habitat (Shuranova *et al.* 2005), to capture and handle food more efficiently (Derby & Atema 1981), and developing a change in acceptability of food (Derby & Atema 1981; Steiner & Harpaz 1987; Daniel & Derby 1988). These habituation behaviours suggest a potential application in conditioning farmed shrimp to the use of automatic feed dispensers as has been observed in finfish aquaculture (e.g. Bratland *et al*. 2010; Zion *et al*. 2010, 2011a,b; Folkedal *et al*. 2018).

In crustaceans, during the first feeding behaviour phases of detection and orientation towards a food source, chemoreceptors on the antennules have been shown to have important roles (Ache 1982; Lee & Meyers 1996). This has been evidenced through the observations of antennule flicking behaviours, where there is rapid movement of the antennules through the surrounding fluid, allowing chemicals to bind repeatedly to receptor sites (e.g. Schmitt & Ache 1979; Derby & Atema 1982; Carr & Derby 1986; Zimmer-Faust 1991; Koehl 2006; Thiel & Breithaupt 2011). A number of studies have observed the greatest antennule flicking frequency at the onset of a stimulus, and is therefore an important feeding behaviour as it indicates chemical perception (e.g. Price & Ache 1977; Schmitt & Ache 1979; Reeder & Ache 1980; Devine & Atema 1982; Allison *et al*. 1992; Gleeson *et al*. 1993). Changes to flicking frequency have been shown to improve the exchange of chemical substances, as

285 flicking movements enhance the discharge of the chemoreceptors, allowing new chemical
286 substances to attach again to the chemoreceptor binding sites (Snow 1973; Schmitt & Ache
287 1979; Atema 1985; Gleeson *et al*. 1993). Decreased flicking may therefore denote an
288 impaired or reduced ability to detect the chemical stimulus and therefore the presence of food
289 (Allison *et al*. 1992; Krång & Rosenqvist 2006; De la Haye *et al*. 2011).
290
291 Antennular flicking in response to chemostimulation is a wide-spread behaviour among
292 crustacean species. For example, increased rates in flicking have been recorded in the giant
293 freshwater prawn (*Macrobrachium rosenbergii* De Man) (to a maximum of 40 flicks/min)
294 when presented with feed with high betaine concentrations (Harpaz & Steiner 1990). Devine
295 and Atema (1982) found that 96% of lobsters (*H. americanus*) maintaining antennular
296 flicking walked in a straight line towards a food source. Reeder and Ache (1980) observed
297 circular movements in the spiny lobster (*P. argus*) when one antennule was ablated.
298 Antennular flicking frequencies of the Dungeness crab (*Metacarcinus magister* Dana) were
299 observed to treble from 20-40 flicks/min to 60-120 flicks/min when individuals were
300 stimulated with different concentrations of clam samples added to the water (Pearson *et al.*
301 1979). Schmitt and Ache (1979) concluded from the same species that an increase in
302 antennular flicking upon detection of a stimulus improved the temporal resolution of
303 chemical sources in the environment. Antennular flicking however varies among crustacean
304 species. Work on the spiny lobster (*P. argus*) observed antennular flicking activity rates
305 between 25 – 90 flicks/min (Daniel & Derby 1991; Goldman & Koehl 2001), whereas
306 Allison *et al*. (1992) observed a maximum rate of 20 flicks/min in the crayfish (*C. bartoni*).
307 The hermit crab (*Pagurus bernhardus* Linnaeus) has been shown to perform flicking rates as
308 high as 140-160 flicks/min (De la Haye *et al*. 2012).
309

An increase in flicking activity, however, is not always necessary and when water moves in a steady flow, crustacean species have been observed to reduce the movement of their antennules (Snow 1975; Goldman & Koehl 2001). Flow type of water can be important and studies with American lobster (*Homarus gammarus* Linnaeus) (Moore *et al*. 1991; Mjos *et al*. 1999) and spiny lobster (*P. argus*) (Wilkens *et al*. 1996; Horner *et al*. 2004) under different turbulent flow regimes observed that antennules change position accordingly. In addition to changes in water flow, possible interferences with chemoreception by substances such as manganese (Engdahl 1997; Krång & Rosenqvist 2006) or sub-optimal culture parameters (i.e. low pH conditions) (Allison *et al*. 1992; De la Haye *et al*. 2011, 2012) can cause changes in antennular flicking activity in crustaceans. Moreover, work with stomatopods, such as mantis shrimp, has shown an increase of antennule flicking activity under low light conditions, when there would be less reliance on visual cues (Cheroske *et al*. 2009). Therefore, such variations in flicking behaviours can produce confusion for researchers identifying behavioural responses towards experimental feeds or additives, and whether affinity between feed and antennule flicking activity is directly related to feeding attraction or if it is moderated by other reasons.

Variation in antennular flicking activities may be a result of different water sampling techniques made by crustaceans. For example, in lobsters, rapid downward motions of antennules may be due to the removal of water previously sampled from the aesthetasc receptors to allow detection of new chemical-bearing water (Goldman & Koehl 2001; Schmidt & Derby 2005). Another characteristic of flicking activity is that, in some cases, it is dependent on crustacean size. Studies on stomatopods found that larger individuals have more rapid chemical diffusion on aesthetasc surfaces than smaller animals (Mead *et al*. 1999). However, this is likely to be species-specific (Goldman & Koehl 2001).

In penaeid shrimp, a limitation in observing the use of antennular flicking is the small size of the shrimp's antennules compared with those of other species, such as lobsters (Pittet *et al*. 1996). However, studies with small hermit crabs (*P. bernhardus*) (3 – 4 cm carapace length) found antennular flicking to be a tractable measure of chemo-responsiveness (De la Haye *et al*. 2012) which demonstrates the potential for observations of *L. vannamei* in similar kinds of studies. The structure and function of the olfactory organs of crustaceans, as a group, is highly congruent (Hallberg *et al*. 1992), therefore, any observed effect in other species such as *H. americanus*, *P. argus* or *P. bernhardus* is likely to occur in other marine crustaceans in a similar way. Nevertheless, there is little information about antennular flicking activity in penaeid shrimp. Moreover, shrimp exhibit more movements of their mouthparts and less of their antennules when compared with both lobsters and crabs (Pittet *et al*. 1996).

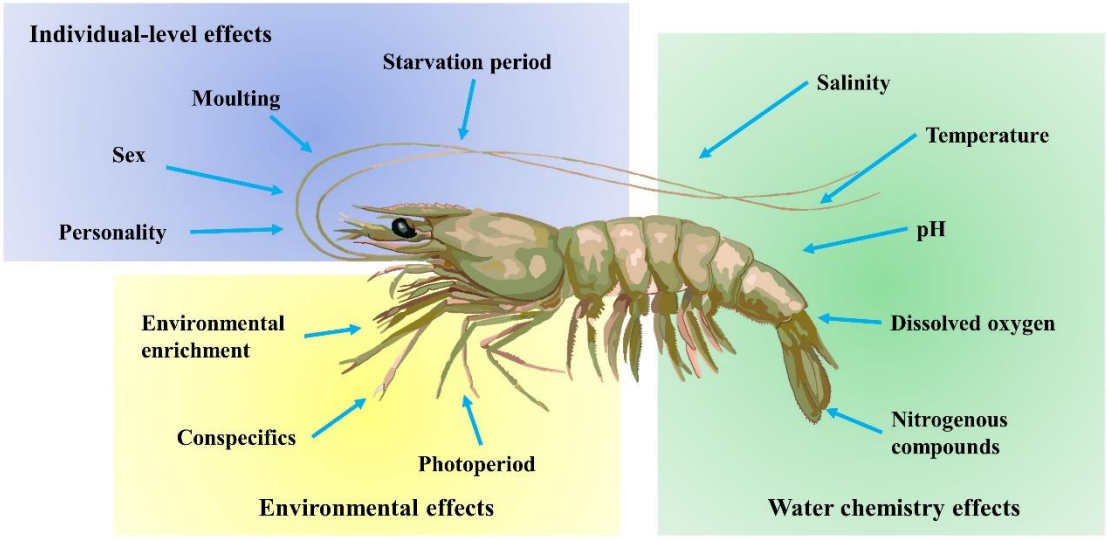
Recognition of food implies its discrimination from non-food items (Hindley 1975), and the elicitation of food-acceptance or food-rejection behaviour is seemingly dependent on a set of chemoreceptors in the dactyl receptors and in the mandibular-oral area (Hazlett 1971; Fuzessery & Childress 1975; Hindley 1975, Robertson *et al*. 1981). Once the crustacean is close to the food source, it makes contact with the food item with the dactyl of the walking leg and moves it towards the maxillipeds and mouthparts. The dactyls of the first two pairs of walking legs bear chemotactic organs which aid with the acceptance process (Ameyaw-Akumfi 1977). Oral handling of feed via the maxillipeds is generally indicated by the disappearance of the food item from the mouthparts and its appearance in the stomach, which can often be observed (Steiner & Harpaz 1987). However, the onset of a feed-handling behavioural pattern does not guarantee that the shrimp will actually go on to consume the feed (Harpaz & Steiner 1987). After feeding, crustaceans present a stereotypic behaviour referred to as antennular grooming (Zimmer-Faust *et al*. 1984; Barbato & Daniel 1997;

Wroblewska *et al*. 2002; Schmidt & Derby 2005). This behaviour has been attributed to the activation of aesthetascs regions through the antennules wiping against maxillipeds and the rubbing movements of maxillipeds against themselves ("auto-grooming") (Barbato & Daniel 1997; Wroblewska *et al*. 2002).

In many species feed rejection behaviours follow a well-defined behavioural pattern. For example, *M. rosenbergii* individuals that go on to reject feed have been observed to make regular movements around food items, with little interaction. Also, any individuals that handled feed in their maxillipeds, made no movements of the mouthparts (Steiner & Harpaz 1987). The hermit crab (*Pagurus granosimanus* Stimpson) has been observed in general to flick the second antennae back and away after contacting the chemical source when food rejection behaviour follows (Wight *et al*. 1990). Food is then pushed away energetically with the chelipeds and the crab backs away from it. In other instances, *P. granosimanus* has been observed to grasp feed hesitantly with the chelipeds before rejecting it.

INFLUENCES ON SHRIMP FEEDING BEHAVIOUR

Understanding shrimp behaviour provides a starting point for refinements to feeding practices, however, there are many influences on shrimp behaviour which are likely to be species and context-specific (Fig. 1). These can be broadly divided into individual level effects, environmental effects and water quality effects.



382

383 **Figure 1.** The influences on shrimp behaviour that are considered likely to affect feeding efficiencies under
384 farmed conditions.

385

386 ## Individual Level Effects

387

388 ***Moulting*** A physiological process whereby crustaceans periodically shed their exoskeleton as
389 a result of their natural growth (Molina-Poveda *et al*. 2002; De Oliveira-Cesar *et al*. 2006;
390 Rusaini & Owens 2011), moulting affects feeding, growth and reproduction (Robertson *et al*.
391 1987; Vega-Villasante *et al*. 2000; Molina-Poveda *et al*. 2002). The moulting process in
392 crustaceans is driven mainly by hormones, but also it is influenced by environmental
393 conditions, developmental stages and physiological states (Chan *et al*. 1988; Cheng *et al*.
394 2002). Penaeids have been observed to suppress feeding activity in the preliminary stages
395 before and during moulting (Dall 1986; Harpaz *et al*. 1987; Chan *et al*. 1988; Dall *et al*. 1990;
396 Vega-Villasante *et al*. 2000; Moss & Moss 2006; Table 1). This cyclic behaviour of non-
397 feeding is termed "physiologic fast" and may be caused by non-functionality of some
398 structures such as the mouth, oesophagus or stomach when an individual sheds the

399 exoskeleton (Vega-Villasante *et al*. 2000). During these periods, penaeids rely on reserves of
400 lipids and carbohydrates to successfully achieve the next moulting phases (Chan *et al*. 1988;
401 Fernández *et al*. 1997). The hepatopancreas is generally considered as the major storage
402 organ in decapod crustaceans, presenting an important role in relation to the accumulation
403 and mobilization of reserves during this time (Allen 1971, Comoglio *et al*. 2004, 2005).
404 Vega-Villasante *et al.* (2000) found that it is possible to calculate the quantity of feed
405 required for shrimp culture according to their moult status and it has been shown in *L.*
406 *vannamei* that the best feed balance and protein efficiency is when shrimp are fed according
407 to their moult cycle (Molina *et al.* 2000).
408
409 There are a range of factors that may influence moulting. Studies in *L. vannamei* have
410 demonstrated the importance of temperature and age. For example, at ranges of 26-30 ºC the
411 average moult cycle length was reported as 4-5 days in juveniles aged 1 month, 10-13 days in
412 2 month-old shrimp and around 15-20 days in 6 month-old sub-adults (De Oliveira-Cesar *et*
413 *al*. 2006). However, Chan *et al*. (1988) performed the same study at 20-22º C with adult *L.*
414 *vannamei* and found moulting cycle length was between 28-40 days. In addition to
415 temperature, environmental conditions such as lunar cycle can modulate and coordinate
416 crustacean physiology (Dall *et al*. 1990; Griffith & Wigglesworth 1993). Molina *et al*. (2000)
417 found that moulting in *L. vannamei* occurred mainly during the new moon cycle in around
418 80% of the population. Similar results were observed in the Northern pink shrimp (*Penaeus*
419 *duorarum* Burkenroad), with a high moulting occurrence close to the full moon event (Fuss
420 & Ogren 1966). The presence of weak levels of dissolved oxygen (DO) or extreme water
421 salinity can also reduce moulting frequency in shrimp through changes in shrimp metabolism
422 (Aquacop *et al*. 1988; Allan & Maguire 1991; Staples & Heales 1991). Culture parameters

423 (i.e. temperature, salinity, dissolved oxygen) are therefore very important in modulating
424 shrimp physiology and behaviour (see section below).
425
426 In terms of behaviour, moulting processes can have substantial effects on overall activity
427 (such as locomotor or swimming activity), but are particularly important in feeding activity
428 (Chan *et al*. 1988). The greatest activity levels are generally observed during the inter-moult
429 phase (Table 1; C). Later, feeding activity is reduced when shrimp are closer to moult in the
430 Pre-moult phase (D) until an inhibition status is reached, however general activity continues
431 to be high. During the moulting process, feeding and general activity levels reach the lowest
432 levels. In the post-moult phase (A-B) shrimp refrain from feeding activities and general
433 activity is restored in accordance to the exoskeleton hardening. Importantly, depending on
434 their moult stage stress can affect shrimp differently; pre-moult (D_2) and post-moult (A)
435 (Table 1) are the phases most sensitive to stress (Robertson *et al.* 1987; Wajsbrot *et al*. 1990),
436 and this can have an additional influence on their overall behaviour.
437
438 **Table 1**. Moulting cycle of penaeid shrimp (*L. vannamei*), indicating changes in overall and feeding activity
439 depending of the phase. Data obtained from Chan *et al*. (1988) and Vega-Villasante *et al*. (2000).
440
441

Phase	Proportion of cycle length (%)	Moulting state	Description	Feeding /Overall
A	2%	Post-Moult	New exoskeleton is very soft, with a parchment texture.	None/Weak
B	4%	Post-Moult	New exoskeleton becomes harder.	None/Restored
C_1	5%	Inter-Moult	New exoskeleton completely formed and resistant.	Restored/Maximal
C_{2-3}	35%	Inter-Moult	Exoskeleton achieves maximum rigidity.	Maximal/Maximal
D_{0-1}	43%	Pre-Moult	Detachment of epithelial cuticle. Secretion of new cuticular layers started.	Decreasing/Maximal

D_{2-3}	11%	Pre-Moult	Colouration of the new cuticular layers. Old exoskeleton soft. Opening of the dehiscence groove. Water is absorbed by shrimp.	None/Maximal
E	-	Moult	Tegument expulsion, shrimp leave exoskeleton. Shrimp body expands.	None/None

Starvation period It is likely that under high stocking densities, depending on the feeding method, some individuals may have reduced access to feed. Crustaceans, however, are generally able to withstand and recover from prolonged periods of starvation (Stuck *et al*. 1996; Hervant *et al*. 1997). Under starvation conditions, *L. vannamei* can reduce their metabolic rate and moulting frequency to save energy (Stuck *et al*. 1996; Comoglio *et al*. 2004). Juvenile *L. vannamei* have been noted to survive up to 15 days under starvation, although an increased mortality rate of 35-45% was recorded during days 9 to 15 (Comoglio *et al*. 2004). As seen during moulting, shrimp reserves are mainly limited to lipids stored in the hepatopancreas (Allen 1971; Comoglio *et al*. 2004, 2005). During starvation, *L. vannamei* uses triacylglycerol (ester lipid) for short periods, but use protein during prolonged starvation periods (Cuzon *et al*. 1980; Stuck *et al*. 1996). During a four-week starvation period the kuruma shrimp (*Penaeus japonicus* Spence Bate) utilised carbohydrates first and then lipids to meet their energy requirements. However, proteins were not utilised until after two weeks of starvation (Cuzon *et al*. 1980). Overall body mass may not be affected due to significant increases in body water content during starvation that occurs so as to maintain body volume and internal turgidity (Wilcox & Jeffries 1976; Cuzon *et al*. 1980; Stuck *et al*. 1996). Recovery after very long starvation periods sometimes cannot be achieved if damage to the hepatopancreas and loss of enzyme synthesis has occurred (Comoglio *et al*. 2004). Starvation level can also influence the ability of shrimp to respond to additional stressors such as

463 hypoxia and salinity changes (Hochachka & Lutz 2001; Palacios *et al*. 2004; Zhang *et al*.
464 2006).
465
466 There is limited information on the impact of starvation period on feeding behaviour in
467 relation to aquaculture. Normally when nutritional studies are carried out, specimens are
468 starved for a period of 18-24 hours (e.g. Holland & Borski 1993; Sanchez *et al*. 2005; Nunes
469 *et al*. 2006; Derby *et al*. 2016). It has been shown that feeding activity and behavioural
470 responses in crustaceans can increase across these time periods (Lee & Meyers 1997). In
471 addition, Sanchez *et al.* (2005) discovered that shorter starvation periods of 18 hours did not
472 constitute enough time to observe an effect on feeding rate and response. This means that
473 variation in starvation periods can influence feeding threshold and subsequent behaviours
474 (Costero & Meyers 1993), with relevance in nutritional studies to test novel attractants for
475 shrimp aquaculture.
476
477 In relation to shrimp farming, high starvation periods are commonly linked to the idea of a
478 decrease in shrimp growth and survival (Stuck *et al*. 1996). However, some studies suggest
479 that starvation followed by re-feeding may improve productivity. For example, Wu and Dong
480 (2002), working with the Chinese white shrimp (*Penaeus chinensis* Osbeck) tested different
481 periods of starvation followed by feeding *ad libitum* (e.g. 1 day starvation:4 days *ad libitum*,
482 2:8 and 4:16). While shrimp subjected to the different combinations showed a faster mass
483 gain during the re-feeding period compared to a control group fed *ad libitum* throughout,
484 after 32 days none of the starved and re-fed reached the same body mass as the controls. Lin
485 *et al*. (2008) reported compensatory growth in *L. vannamei* 3 – 9 days after short periods of
486 starvation (1 – 3 days). Moreover, Maciel *et al*. (2018) suggest restricted feed programs in
487 shrimp aquaculture can reduce operating costs (i.e. labour and feeding costs) and improve the

pond water quality. These strategies, however, have to be properly controlled as starvation can affect negatively shrimp productivity (i.e. lower growth and survival) and induce negative behaviours such as cannibalism (Martin *et al*. 1998; Kautsky *et al*. 2000; Arnold *et al*. 2006; Zhang *et al*. 2010).

Sex differences In penaeid shrimp, females are larger than males (Moss *et al*. 2002; Campos-Ramos *et al*. 2006; Moss & Moss 2006; Gopal *et al*. 2010) due to a greater gain in mass per moult cycle (Hansford & Hewitt 1994). This is most likely caused by different biological requirements at the onset of sexual maturation (Pérez-Rostro & Ibarra 2003). Penaeids possess a stable genetic sex determination system, not determined by environmental conditions as in some crustacean taxa such as copepods and amphipods (Legrand *et al*. 1987). In *L. vannamei*, sexual size dimorphism begins at approximately 10 g (Chow & Sandifer 1991) and becomes significant around 17 g (Pérez-Rostro *et al.* 1999; Pérez-Rostro & Ibarra 2003). Females are generally heavier than males with a larger cephalothorax and a wider first abdominal segment (Chow & Sandifer 1991; Pérez-Rostro *et al*. 1999, Pérez-Rostro & Ibarra 2003), and a study by Accioly *et al*. (2013) determined the possibility of recognising sexual dimorphism in *L. vannamei* using geometric morphometrics in these structures.

Studies on *P. monodon* (Hansford & Hewitt 1994; Gopal *et al*. 2010) and *L. vannamei* (Moss *et al*. 2002; Moss & Moss 2006) suggest that female monosex cultures grow faster than mixed-sex cultures or male monosex cultures. However, there are very few studies in penaeids that relate variation in behaviour to sexual differences. Moss and Moss (2006) observed that *L. vannamei* males were more active swimmers than females, which normally spent most time on the bottom of tanks. Moreover, males presented more aggressive behaviours than females when competing for food. Males tended to monopolise the food

source for more time than females, even though they were smaller. It is therefore clear that gender is a more important factor than size for explaining variations in feeding activity in this species. It appears that *L. vannamei* females do not have a competitive advantage over food, one of the possible causes of sexual growth dimorphism in this species is physiological advantage (Moss & Moss 2006). For example, Hansford and Hewitt (1994) reported that *P. monodon* females had a lower feed conversion ratio and a more efficient digestibility of food energy compared to males. At the same time, males could have a greater metabolic rate and/or stress levels than females (Taylor *et al*. 2004; Moss & Moss 2006). This could explain the higher aggressiveness and feeding activity observed in males, behaviour that has also been recorded in other crustaceans such as rock shrimp (*Rhynchocinetes typus* H. Milne Edwards) (Dennenmoser & Thiel 2007) and American lobster (*H. americanus*) (Karavanich & Atema 1998) as well as other finfish aquaculture species such as Atlantic salmon (*Salmo salar* Linnaeus) (Cutts *et al*. 1998) and rainbow trout (*Oncorhynchus mykiss* Walbaum) (Metcalfe 1986). However, the paucity of information makes it difficult to make definitive conclusions here and more research is required.

Personality Behaviour is perhaps the most flexible phenotypic feature, offering the quickest response of animals to unexpected events in a variable environment (Hazlett 1995). This phenotypic plasticity allows appropriate responses to changing conditions or situations (Sih *et al*. 2004; Dingemanse *et al*. 2010), having major impacts on individual fitness (Sih *et al*. 2004; Gherardi *et al*. 2012; Briffa *et al*. 2015). However, it is also evident that phenotypic plasticity might present some constraints with regards to sensory capabilities, morphological limitations or limits on learning abilities (Hazlett 1995; DeWitt *et al*. 1998; Briffa *et al*. 2015; Briffa & Sneddon 2016). Such limits on behavioural plasticity appear to vary between and within populations (Wilson 1998), leading in some cases to variation in behaviour between individuals (Briffa *et al*. 2008; Briffa *et al*. 2015). Such variations in behaviours may be

538 considered as ‘personality’ traits when they are observed to be consistent and repeatable in
539 individuals across time in different contexts (e.g. feeding, mating) and situations (e.g.
540 presence of food or predators) (Briffa & Weiss 2010; Briffa & Twyman 2011; Gherardi *et al*.
541 2012). In many studies, individuals are distinguished based on the ‘shyness-boldness axis’
542 defined by Wilson *et al*. (1993). Combinations of behaviours that occur across different
543 situations and contexts with behavioural consistency within individuals of a population may
544 also be observed and are described as ‘behavioural syndromes’ (Gherardi *et al*. 2012; Briffa
545 *et al*. 2015).

546 Reliable, repeatable individual variation in behaviour, or animal personality, has been
547 reported in a wide group of taxa including mammals, birds and fish. Recent studies have also
548 uncovered repeatable behavioural differences in invertebrates such as arachnids, cnidarians
549 and crustaceans (see Reviews of Dingemanse *et al*. 2010 and Gherardi *et al*. 2012). In
550 crustaceans, evidence for bold and shy individuals has been found in the hermit crab *P.*
551 *bernhardus* where bold individuals showed high levels of exploratory behaviour in a new
552 environment, investigated novel objects and when disturbed showed a sudden startle response
553 of short duration (Briffa *et al*. 2008). Similarly, Vainikka *et al*. (2011) observed personality
554 traits in crayfish (*Astacus astacus* Linnaeus) and proposed that boldness in this species
555 influences predatory risk and intraspecific competition.

556 The occurrence of personality traits in crustacean aquaculture, particularly in penaeid shrimp,
557 may be important in the context of feeding where bolder individuals might be more likely to
558 interact with feed and consume it at a faster rate. Currently there is no evidence to support
559 this within shrimp aquaculture, however, in finfish aquaculture some studies highlight the
560 presence of personalities and copying styles (stress responses) which can provide advantages
561 for culture, for example in establishing selection-based breeding programmes or improving

562 domestication (Castanheira *et al*. 2013; Ibarra-Zatarain *et al*. 2016). It may also be possible to
563 link proactive (bold) individuals with important aquaculture outputs, such as growth, disease
564 resistance, food conversion, or survival (Ibarra-Zatarain *et al*. 2016). Therefore,
565 understanding the role of animal personality in commercial settings may be of great
566 importance in optimising production (Huntingford & Adams 2005).

567 **Environmental Effects**

568

569 ***Environmental enrichment*** As benthic animals, shrimp are mainly constrained to two-
570 dimensional space rather than three-dimensional volume (Kumlu *et al*. 2001), although when
571 shrimp are stocked at high densities the water column becomes more important as they can
572 feed on suspended food particles (Tacon *et al*. 2013). Therefore, bottom substrate becomes an
573 important concern in an aquaculture setting. Several studies have demonstrated that artificial
574 substrates could increase the food supplement for shrimp (i.e. enhance the colonisation of
575 epiphytic biota) (Thompson *et al*. 2002; Burford *et al*. 2004; Moss & Moss 2004; Arnold *et*
576 *al*. 2005, 2006) as well as improve the water quality and control pathogenic bacteria
577 (Bratvold & Browdy 2001; Thompson *et al*. 2002; Moss & Moss 2004; Ballester *et al*. 2007;
578 Kumar *et al*. 2017). In *L. vannamei* the addition of artificial substrates has improved growth
579 and/or survival of postlarvae and juveniles, even at high stocking densities (Bratvold &
580 Browdy 2001; Moss & Moss 2004; Zarain-Herzberg *et al*. 2006). For example, Bratvold &
581 Browdy (2001) indicated that, in tanks containing AquaMats^{TM}, *L. vannamei* individuals
582 were up to 30% heavier than in tanks without mats.

583

584 Artificial substrates may confer several potential behavioural benefits for shrimp culture by
585 providing refuge for moulting shrimp, reducing aggressive interactions (e.g., cannibalism)
586 and increasing the surface area on which shrimp graze (Moss & Moss 2004; Arnold *et al.*

587 2006). It has also been suggested that for species that exhibit burrowing behaviour, sediment
588 may be required for optimal production (Allan & Maguire 1995). Some studies have shown
589 little burrowing activity exhibited by *L. vannamei* (Boddeke 1983; Robertson *et al*. 1993;
590 Pontes & Arruda 2005a,b; Zhang *et al*. 2010; Da Costa *et al*. 2016;), thus the presence of
591 sediment may have relatively little effect on its growth and behaviour (Bratvold & Browdy
592 2001). However, information is scarce and more research on this topic is needed, as
593 according to Moctezuma and Blake (1981) *L. vannamei* shows a clear burrowing activity
594 during diurnal hours and emerge at night, as do other *Penaeus* spp. (Hindley 1975; Boddeke
595 1983; Nunes *et al*. 1996). Moreover, Zhang *et al*. (2010) found behavioural changes in *L.*
596 *vannamei* in relation to artificial substrates, demonstrating a clear change in shrimp
597 distribution between tanks with and without artificial substrate. The proportion of shrimp on
598 the bottom of tanks with artificial substrates was significantly lower than tanks without
599 artificial substrates, with the differences becoming more distinct with a longer rearing time.
600 This provides evidence of how artificial substrates can disperse shrimp from tank bottoms
601 and thus alleviate the negative effect of high stocking density on shrimp production. The use
602 of artificial substrate may also benefit feeding efficiency, stimulating more natural
603 behavioural processes. Moreover, the role of artificial substrates in relation to the production
604 of natural food supplement could encourage *L. vannamei* feeding activity.
605
606 ***Conspecific presence*** The presence of conspecifics and stocking density is an important
607 consideration in aquaculture production. Normally, when held in higher densities, shrimp
608 exhibit a reduction in growth and survival as a result of a combination of different factors
609 including a decrease in favourable space and natural food sources and an increase in adverse
610 behaviour such as cannibalism (Martin *et al*. 1998; Kautsky *et al*. 2000; Arnold *et al*. 2006;
611 Zhang *et al*. 2010). It is also obvious that feeding success is density-dependent (Chavanich *et*

612 *al*. 2016) therefore stocking density is an important aspect when considering feeding
613 behaviour patterns (Da Costa *et al*. 2016). In general, *L. vannamei* is amenable to culture at
614 very high densities from 60 to 150 individuals/m^2 in pond culture, and even as high as 400
615 individuals/m^2 in controlled recirculated tank conditions (Briggs *et al*. 2004; Funge-Smith &
616 Briggs 2005). Such intensive culture systems, however, require a much higher degree of
617 control over environmental parameters (Briggs *et al*. 2004; Funge-Smith & Briggs 2005).
618 Moreover, high densities can compromise feeding management of shrimp production, as high
619 densities have more competition for access to feeding trays and that can restrict the number
620 of shrimp feeding (Sanchez *et al*. 2005). Therefore, feed management strategies need to be
621 implemented and automatic feed dispensers may present a promising solution to restricted
622 feeding at high densities by means of dispensing smaller amounts of feed many times a day
623 (Jory 2016). Stocking density affects growth of *L. vannamei* (Balakrishnan *et al*. 2011), and
624 stronger density-growth relationships have been observed at medium and higher densities (40
625 – 150 individuals/m^2) than at moderately low densities (5 - 40 individuals/m^2) (Sandifer *et al*.
626 1987, 1988; Wyban *et al*. 1987, 1988). According to Wyban *et al*. (1988), *L. vannamei*
627 shrimp stocked at a density of 45 individuals/m^2 presented an excellent growth and survival
628 rate, however at higher densities *L. vannamei* can often show an aggressive feeding
629 behaviour when food sources are limited (Zhang *et al*. 2010). Nevertheless, once again, this
630 may be mitigated through appropriate feed management.
631
632 There has been limited work conducted on the effects that different stocking densities have
633 on behaviours of *L. vannamei*. Da Costa *et al.* (2016) found that groups at low (50
634 individuals/m^2), medium (75 individuals/m^2) and high density (100 individuals/m^2) displayed
635 differences in their individual behaviours. With regards to feeding, medium densities had the
636 lowest feeding frequency of all groups. Higher densities were observed to have a medium

feeding efficiency and lower densities performed best in terms of feeding (Da Costa *et al.* 2016). With regards to other behaviours, the study noted that there were, however, few swimming behaviours at lower densities compared to higher stocking densities, most likely as a trade-off due to increased feeding. As high frequency of swimming behaviour in *L. vannamei* has been shown to be associated with stress (Taylor *et al*. 2004), it is also possible that animals at a lower stocking density moved less frequently due to less chemical, tactile or visual interference by other individuals.

Photoperiod In crustacean aquaculture, light conditions and photoperiod play important roles in both behaviour (e.g. Pontes 2006; Santos *et al*. 2016) and physiology (e.g. Nakamura & Echavarria 1989; Pontes & Arruda 2005b; Ravi & Manisseri 2013). Light conditions are probably the most important single factor for determining the locomotor activity in penaeid shrimp (Dall *et al*. 1990; Wassenberg & Hill 1994), therefore understanding the behaviours which result in the activity pattern of species such as *L. vannamei* during the day/night is vital for determining feeding schedules in aquaculture (Pontes 2006).

In general, penaeids exhibit circadian rhythms which are linked with diurnal burrowing habits and emergence from the substratum in the dark (Hindley 1975; Boddeke 1983; Nunes *et al*. 1996). For example, *P. japonicus* is naturally active at night therefore captive animals are usually fed after sunset (Nakamura & Echavarria 1989). However, *L. vannamei* belong to the group of non-burrowing shrimp, and are likely to exhibit the same feeding and locomotor activity during the day as well as at night, and do not usually burrow during the daytime (Boddeke 1983; Robertson *et al*. 1993; Pontes & Arruda 2005a,b; Zhang *et al*. 2010; Da Costa *et al*. 2016). However, some studies suggest feeding behaviour in *L. vannamei* is heightened under light conditions. This may be a result of temperature fluctuations, with low

night-time water temperatures relative to the daytime temperatures reducing the activity of the shrimp (Robertson *et al*. 1993). Additionally, *L. vannamei* seems to be less motile under strong light than weak light conditions (Zhang *et al*. 2006). Sanudin *et al*. (2014) examined *L. vannamei* larvae (0.5cm total length (TL)) and demonstrated a greater ingestion rate of feed in light conditions compared to dark. As the shrimp grew (up to 1 – 1.5 cm TL), differences between light and dark conditions did not influence the feeding activity to the same degree. These findings may reflect the ontogenetic development of chemoreceptors to find food sources compared to larvae stages that rely more on vision (Sanudin *et al*. 2014). However, more research into ontological changes in chemoreception vs vision is necessary and presents an exciting area for future studies.

The effect of light on feeding and growth efficiency may be dependent on whether trials are located indoors or outdoors. For example, *L. vannamei* juveniles had better feeding and growth efficiency during the light hours in trials performed inside (Robertson *et al.* 1993; Tacon *et al.* 2002; Pontes & Arruda 2005b; Pontes *et al.* 2006). However outdoor trials found no significant differences between diurnal and nocturnal food consumption patterns (Nunes *et al.* 1996; Tacon *et al.* 2002). Regardless of these findings, *L. vannamei* shows the highest ingestion of feed around the middle of the light phase (Lima *et al.* 2009) and it has been determined that feed should be offered in the light phase and at a greater proportion 7 hours after sunrise (Pontes *et al*. 2006). Substrate exploration behaviour in *L. vannamei*, indicative of the search for feed, was more intense around this time (Pontes 2006). Moreover, some studies have demonstrated the possibility of synchronising feeding activity with shrimp circadian rhythms (Miguel & Aréchiga 1994; Santos *et al*. 2016); understanding such behavioural rhythms is critical for feeding management for species such as *L. vannamei*. For example, Santos *et al*. (2016) showed that the use of automatic self-feeding systems by *L.*

687 *vannamei* individuals was influenced by their circadian rhythms (i.e. shrimp activated the
688 feeders more at night). This information may have potential implications for commercial
689 systems that distribute feed automatically to shrimp (sometimes over 24 hours), a method
690 increasing in popularity in shrimp farms (Jory 2016; Molina & Espinoza 2018).
691
692
693 **Water Quality Effects**
694
695 ***Salinity*** Salinity is one of the most basic environmental parameters of marine shrimp culture
696 (Zhang *et al*. 2006). In general, euryhaline decapod crustaceans acclimated to sea water are
697 osmoconformers although some groups, such as the penaeid shrimp, have the capacity to
698 osmoregulate (Dall 1981; Dall *et al*. 1990). Osmotic regulation in penaeid shrimp is a
699 physiological property which can determine their distribution under different salinities
700 (Charmantier 1987; Vargas-Albores & Ochoa 1992). In *L. vannamei* the osmoregulatory
701 ability is better in juvenile phases, mostly at low salinities, declining naturally when they
702 reach subadult or adult stages (Gong *et al*. 2004; Bett & Vinatea 2009). This is reflected in
703 their natural distribution where postlarvae and juveniles inhabit brackish water but migrate as
704 adults to marine habitats (Vargas-Albores & Ochoa 1992; Ponce-Palafox *et al*. 1997). In
705 addition, size differences within a species may also affect the osmoregulatory capacity, with
706 smaller individuals being better regulators than those that are larger (Vargas-Albores &
707 Ochoa 1992).
708
709 The isosmotic point has been associated with optimum conditions for growth in penaeid
710 shrimp (between 20 – 25 ppt), however *L. vannamei* grows particularly well at low salinities
711 of around 10 – 20 ppt, below isosmotic conditions (Wyban & Sweeny 1991; Bray *et al*. 1994;

712 Rosas *et al*. 2001; Bett & Vinatea 2009; Ponce-Palafox *et al*. 2013). However, *Litopenaeus*
713 *vannamei* tolerates a wide range of salinities from 0.5 -50 ppt (Charmantier 1998; Briggs *et*
714 *al*. 2004; Funge-Smith & Brigss 2005; Bett & Vinatea 2009), levels that are currently found
715 within shrimp farming. Moreover, this ability makes the species a good candidate for inland
716 farms where they may be subject to high salinity fluctuations over a 24 hour period (Anger
717 1996; Díaz *et al*. 2001; Briggs *et al*. 2004; Funge-Smith & Briggs 2005).
718
719 In terms of how behaviour may be affected by salinity, there are a number of studies which
720 can provide better understanding. Gleeson *et al*. (1996) found that under low salinity
721 concentrations (< 12.5 ppt) or fresh water conditions (0 ppt) the functioning of the
722 aesthetasc/olfactory sensilla in crustaceans can be compromised, resulting in a decrease in
723 detection capacity. Rosas *et al.* (2001) found an increase in locomotor activity when *L.*
724 *vannamei* juveniles were maintained under 10 ppt. This may indicate an escape response to
725 those environmental conditions, as *L. vannamei* individuals reared under low salinity
726 conditions present low stress tolerance (Li *et al.* 2007). Davis *et al*. (2002) found similar
727 effects of low salinity where *L. vannamei* individuals were mainly found at the sides of the
728 tanks, displaying lethargic behaviours and a greater sensitivity to stress caused by handling,
729 temperature changes and low dissolved oxygen. There is little information on how feeding
730 behaviour is affected across different salinities, however, studies note a clear effect of salinity
731 on oxygen consumption for *L. vannamei*, which is related to feeding activity (i.e. higher
732 oxygen consumption/respiratory metabolism increases feeding activity). Nevertheless, this
733 relationship remains unclear as some studies observed a direct increase between oxygen
734 consumption and salinity concentration (e.g. Bett & Vinatea 2009; Zhang *et al*. 2009; Ponce-
735 Palafox *et al*. 2013) and others an inverse relationship between them (e.g. Rosas *et al*. 2001;

Li *et al*. 2007; Li *et al*. 2017). It is clear that further research is necessary to fully understand the effect of salinity on shrimp behaviour.

Temperature Another important environmental factor influencing feeding and overall metabolic rate in marine invertebrates is temperature (Kinne 1966; Armitage & Wall 1982; Wyban *et al*. 1995; Magallón-Barajas *et al*. 2006), particularly in organisms with life cycles involving estuarine areas that experience large temperature oscillations (Darsey 1990). In *L. vannamei*, temperature and temperature-salinity interactions are the main factors modulating growth, feeding rate and oxygen consumption (Wyban *et al*. 1988, 1995; Ponce-Palafox *et al*. 1997; Díaz *et al*. 2001; Ponce-Palafox *et al*. 2013). Several studies have concluded that oxygen consumption between 24-30º C (at salinities of 15-25 ppt) results in greater stability for *L. vannamei* cultures (Villarreal *et al*. 1994; Bett & Vinatea 2009; Valenzuela-Quiñonez *et al*. 2011; Ponce-Palafox *et al*. 2013). Moreover, this temperature range overlays with the optimal growth rate of the species (Wyban *et al*. 1995; Briggs *et al*. 2004). These temperatures are normally associated with the native distribution of *L. vannamei* on the Pacific coast. However, *L. vannamei* is able to tolerate a wide range of temperatures, from as low as 15º C up to 33º C, but at reduced growth rates (Wyban & Sweeny 1991; Funge-Smith & Briggs 2005). This adaptation is advantageous because juvenile *L. vannamei* often inhabit semi-enclosed or closed estuaries and rock pools that are subject to high temperature fluctuations over a 24 hour period (Anger, 1996). Tolerance of lower temperatures allows culture during the cold season (October-February) in the Northern hemisphere (Briggs *et al*. 2004; Funge-Smith & Briggs 2005).

In the context of feeding behaviour, temperature has a considerable effect across all size classes. Feeding rates and subsequent growth of *L. vannamei* are directly correlated with

761 temperature and fluctuate inversely with size (Wyban *et al*. 1995), with shrimp cultured at
762 higher temperatures growing faster as their metabolic rates are accelerated (Gong *et al*.
763 2004). According to Ponce-Palafox *et al*. (1997), juveniles of *L. vannamei* exhibited low food
764 consumption at 20º C compared with hyperactive animals at 35º C (salinities > 20 ppt).
765 Moreover, when they were offered unlimited food, shrimp maintained at 35º C had the
766 highest rate of food consumption. Wyban *et al*. (1995) found the same temperature effects in
767 relation to feeding activity and growth, particularly between 23 – 27º C, with shrimp being
768 extremely sensitive to small temperature changes. The study also concluded that *L. vannamei*
769 culture at low temperature conditions (23º C) resulted in problems in growth associated with
770 feeding activity which could be solved through use of more attractive diets. Hernández *et al*.
771 (2006) observed that the preferred feeding temperature of *L. vannamei* was within 26 – 31º C,
772 and according to Cuéllar-Anjel *et al*. (2010) feeding should be conducted at temperatures
773 above 26º C.
774
775 ***pH*** The pH of body fluids governs the ionization state of proteins and their physiological
776 function, and its control is vital for the proper functioning of animals (Reeves & Rahn 1979).
777 Studies have demonstrated the adverse effect of changes in pH on the chemo-responsiveness
778 of crustaceans (e.g. Allison *et al*. 1992; De la Haye *et al*. 2011, 2012), which have important
779 implications for feeding behaviour. Moreover, abnormal pH values have been reported to
780 cause a wide range of problems across a variety of crustacean species such as stunted growth
781 and reduced survival (Allan & Maguire 1992; Wang *et al*. 2002; Chen & Chen 2003; Wang
782 *et al*. 2009), disturbed ionoregulation (Morgan & McMahon 1982; Allan & Maguire 1992),
783 acid-base imbalance (Morgan & McMahon 1982), DNA damage (Wang *et al*. 2009) and
784 abnormal behaviours (Allison *et al*. 1992; Das & Sahu 2005). Therefore, controlling pH is
785 important due to the large potential fluctuations that may occur in aquaculture ponds.

The majority of studies on *L. vannamei* utilise pH parameters in the range of 7.4 – 8.2 (Samocha *et al*. 2004b; Zhang *et al*. 2006; Grey *et al*. 2009; Wang *et al*. 2009; Da Costa *et al*. 2016), and it has been found that changes in pH have important implications for survival. For example, Wang *et al*. (2009), found 100% survival across a 24 hour period for *L. vannamei* under conditions at pH 7.4. Survival was reduced however to 65% under more acidic conditions (pH 5.6) and 35% under more alkaline conditions (pH 9.3). With regards to feeding behaviours, a number of effects due to changes in pH have been identified in crustaceans. Initially, low pH may reduce chemoreceptive perception by modifying the charge distribution on the chemoreceptor cells of crustacean sensory organs (Tierney & Atema, 1988). Moreover, changes in chemo-responsiveness might simply reflect reduced activity levels, or reduced motivation to respond to chemical cues, occurring as a result of the elevated metabolic load of maintaining acid-base balance under conditions of low pH (Spicer *et al*. 2007). There may also be direct physical damage to the sensory organs as a result of low pH conditions (De la Haye *et al*. 2012). Additionally, it has been shown that crustaceans in low pH conditions significantly reduce antennular flicking which triggers less locomotor activity, lack of stimulation and metabolic depression (Allison *et al*. 1992; De la Haye *et al*. 2011, 2012). For example, reduced pH compromises resource assessment and decision-making behaviour in European hermit crabs (*P. bernhardus*) (De la Haye *et al*. 2011). Allison *et al*. (1992) found similar results in freshwater crayfish (*C. bartoni*), which flicked its antennules at a reduced rate and failed to locate a food source under low pH conditions (4.0) instead of normal pH conditions (7.5). Therefore, the decreased flicking observed under low pH conditions could imply a reduced ability to detect the chemical stimulus (De la Haye *et al*. 2011).

Dissolved oxygen Dissolved oxygen (DO) is a major limiting factor in crustacean aquaculture (Martinez-Palacios *et al*. 1996; Cheng *et al*. 2003; Pérez-Rostro *et al*. 2004; Zhang *et al*. 2006). During the initial phases of shrimp development (larvae and juvenile forms), it is vital to maintain adequate oxygen levels (Bett & Vinatea 2009). The bottom layer of pond waters, where shrimp mostly remain, may become hypoxic or even anoxic due to decomposition of accumulated organic matter and organism respiration (Cheng *et al*. 2003; Zhang *et al*. 2006). Normally, DO values higher than 5 mg l^{-1} have been suggested for intensive culture practices (Cheng *et al*. 2003). Low DO concentrations negatively affect the behaviour and physiology of crustaceans, such as growth, survival, respiration and circulation, metabolism, moulting and feeding (Seidman & Lawrence 1985; Clark 1986; Aquacop *et al*. 1988; Allan & Maguire 1991).

The effect of hypoxia on growth, survival, feeding, moulting, behaviour, osmoregulatory capacity and immune response of *L. vannamei* has been documented by some authors (Aquacop *et al*. 1988; Hopkins *et al*. 1991; Charmantier *et al*. 1994; Pérez-Rostro *et al*. 2004; Zhang *et al*. 2006). *Litopenaeus vannamei* tolerates low DO levels, although it does not grow well below 2.8 - 3 mg l^{-1}, which is considered the limit of hypoxic conditions (Martinez-Palacios *et al*. 1996; Vinatea *et al*. 2009). Lethal DO levels for *L. vannamei* are between 0.2 – 1 mg l^{-1} (Hopkins *et al*. 1991; Pérez-Rostro *et al*. 2004) and it appears *L. vannamei* is an oxygen conformer with modification to respiratory rate detected when DO levels decreased below 5 mg l^{-1} (Martinez-Palacios *et al*. 1996). It is possible to control some characteristics of *L. vannamei* cultures to improve their resistance against hypoxic conditions. Zhang *et al*. (2006) concluded that certain water parameters (22º C, 16.6 ppt salinity, pH 7.6) and strong light conditions can help to counteract the effects of low DO levels. Nevertheless, exposure

834 time at low DO or high culture densities has a cumulative effect on the mortality rate or on
835 subsequent performance after recovery (Pérez-Rostro *et al*. 2004; Vinatea *et al*. 2009).
836
837 Under hypoxia, individuals respond by decreasing energy production as well as changes to
838 behaviour (Pérez-Rostro *et al*. 2004). Changes in general locomotor behaviour in *L.*
839 *vannamei* have been observed during hypoxic periods. When DO is at 50% saturation, *L.*
840 *vannamei* exhibits an increase in activity, making short but frequent random swimming
841 movements. Once the saturation value is below 50%, activity decreases, with slower
842 swimming speeds but with a clear and evident pattern of surface-seeking behaviour (Zhang *et*
843 *al*. 2006). Finally, activity ceases when DO levels fall below 1 mg l^{-1} (lethal concentration)
844 (Allan & Maguire 1991; Pörtner *et al*. 2004; Zhang *et al*. 2006). This reduction in activity
845 may be a result of increased lactate concentrations in muscle and hepatopancreas after
846 exposure to hypoxic conditions (Mauro & Malecha 1984; Pérez-Rostro *et al*. 2004).
847 Additionally, shrimp exhibit increased ventilatory activity in low oxygen conditions
848 (Martinez-Palacios *et al*. 1996), which enhances CO_2 excretion from the haemolymph,
849 resulting in increased blood pH (Hagerman & Uglow 1984, 1985; Mauro & Malecha 1984).
850
851 There is little information on feeding behaviour and how it is affected by fluctuations of DO.
852 Cuéllar-Anjel *et al*. (2010) concluded that when DO concentrations fall below 4.5 mg/L
853 reduced feed consumption in *L. vannamei* occurs. In addition, if DO concentration is low for
854 a period of time (days or weeks), daily feed rations should be recalculated with the aim of
855 reducing or suspending feeding until normal water DO levels are attained.
856
857 ***Nitrogenous compounds*** Ammonia is the main nitrogenous end-product excreted by
858 crustaceans (Dall *et al*. 1990), and decomposing organic solids (e.g. uneaten food) can

produce an additional source of ammonia inside aquaculture systems (Chen & Lei 1990). Therefore, nitrogenous compound concentration is directly correlated with stocking density (Martin *et al*. 1998). Ammonia is utilised as a substrate by autotrophic nitrifying aerobic bacteria, *Nitrosomas* and *Nitrobacter*, which oxidize it to nitrite and nitrate, respectively (Chen & Kou 1992, Montoya *et al*. 2002). According to Martin *et al*. (1998), up to 38% of the nitrogen entering ponds via the inflow and in feed pellets could accumulate in the sediment, although it depends on the system used (e.g. biofloc systems can maintain nitrogenous compounds at safe levels) (Vinatea *et al*. 2009; Maicá *et al*. 2014). *Litopenaeus vannamei* presents a higher tolerance to total ammonia nitrogen (TAN) levels than other penaeid shrimp species (Frías-Espericueta *et al*. 1999; Lin & Chen 2001; Schuler *et al*. 2010), presenting a 96 hours LC50 with concentrations as high as 39.54-70.9 mg/l at high salinity conditions (34-35 ppt) (Frías-Espericueta *et al*. 1999; Lin & Chen 2001). In addition, *L. vannamei* also shows an increased tolerance to ammonia with age (Frías-Espericueta *et al*. 2000). However, this tolerance to ammonia can be compromised depending on culture parameters. For example, it has been observed that TAN tolerance decreased to 24.39 mg/l when salinity dropped to 15 ppt (Lin & Chen 2001) or to 9.33 mg/l at a salinity of 3 ppt (Li *et al*. 2007). Low salinities may therefore increase ammonia excretion in penaeid shrimp (Rosas *et al*. 1999), resulting in higher susceptibility of *L. vannamei* to ammonia toxicity with salinity levels below 5 ppt (Li *et al*. 2007). Similarly, at high pH levels (pH 9) ammonia may become very toxic for *L. vannamei* (Magallón-Barajas *et al*. 2006).

The accumulation of nitrogenous compounds inside culture systems can produce a series of non-beneficial effects, such as immune suppression and disease incidence (Liu & Chen 2004), physical damage (e.g. hepatopancreas, gills) (Kuhn *et al*. 2010; Furtado *et al*. 2015), cessation of feeding and growth (Frías-Espericueta *et al*. 2000), which result in higher

884 mortality rates in penaeid shrimp (Chen & Lei 1990). These setbacks mean the accumulation
885 of nitrogenous compounds is one of the most limiting parameters within shrimp aquaculture.
886 For that reason, safe levels of TAN, nitrites and nitrates for rearing *L. vannamei* were
887 estimated to be 2.44, 6.1 and 145 mg/l, respectively, at low salinities and 3.95, 25.7 and 177
888 mg/l at high salinities (Lin & Chen 2001, 2003; Kuhn *et al*. 2010; Furtado *et al*. 2015). When
889 ammonia levels are high, the first reaction of penaeids is the reduction or cessation of feeding
890 which in turn reduces the production of metabolic ammonia (Colt & Armstrong 1981).
891 Moreover, according to ammonia concentration increases in the water, the ammonia excreted
892 by shrimp is reduced. Consequently, the ammonia level in blood and tissues increases with
893 deleterious effects on the shrimp physiology and metabolism (Frías-Espericueta *et al*. 2000;
894 Barbieri 2010). This is directly connected with how ammonia affects growth negatively in
895 penaeid shrimp. For example, Wickins (1976) reported ammonia concentrations as small as
896 0.22-0.69 mg/l can reduce growth in several penaeid shrimp species by 50%. Chen and Kou
897 (1992) found in *P. japonicus* juveniles that 40 days of 30 mg/l of ammonia produced a 86%
898 reduction in mass gain and a 17% reduction in length compared to controls. Furthermore,
899 there appears to be an important correlation between higher TAN levels and lower feeding
900 activity, although more research into effects of nitrogenous compounds on specific feeding
901 behaviours is required.
902
903
904 **HOW CAN WE USE BEHAVIOUR TO IMPROVE SHRIMP AQUACULTURE?**
905
906 Ethological studies in the context of shrimp farming are limited (e.g. Primavera & Lebata
907 1995; Soares *et al*. 2005; Silva *et al*. 2012; Da Costa *et al*. 2016), with those related to
908 feeding behaviour generally investigating responses to chemical stimulants (e.g. Costero &

909 Meyers 1993; Pittet *et al*. 1996; Nunes *et al*. 2006). The importance of chemical cues in
910 identifying and orientating towards potential food sources means that commercial diets must
911 be chemically attractive and include specific chemical cues that can be rapidly recognized as
912 a food source and initiate shrimp feeding behaviour (Zimmer-Faust 1989; Sanchez *et al*.
913 2005; Grey *et al*. 2009). Feeding effectors (attractants and palatability factors) are compounds
914 that attract animals via chemical stimuli and enhance palatability of food (Lee & Meyers
915 1997; Smith *et al*. 2005; Suresh *et al*. 2011). As such, compounds that can enhance feeding
916 behaviour have received a lot of attention as a potential refinement in crustacean aquaculture
917 (e.g. Hartati & Briggs 1993; Smith *et al*. 2005; Nunes *et al*. 2006; Grey *et al*. 2009),
918 especially for species such as *L. vanmamei* (Heinen 1980; Costero & Meyers 1993; Gadient
919 & Schai, 1994; Peñaflorida & Virtanen 1996; Nunes *et al*. 2006). Table 2 summarises feeding
920 studies in shrimp which have examined the use of potential feed effectors. Feeding attractants
921 can elicit behavioural and physiological responses from the shrimp's olfactory and gustatory
922 systems, stimulating the different feeding behaviour phases discussed above (Lee & Meyers
923 1996) (see behavioural responses section). For example, a range of food effectors tested by
924 Nunes *et al*. (2006) in *L. vannamei* resulted in improved feeding efficiency correlated with
925 reduced time spent on perception, orientation and locomotion, and more time spent feeding.
926
927 In addition to the chemical utilised, it is important to consider the amount which is used in
928 feed (i.e. the inclusion level) when understanding effects on behaviour. Obviously, the level
929 of feed enhancer needs to be high enough to stimulate shrimp behaviour (Nunes *et al*. 2006).
930 Derby *et al*. (2016) found a positive relationship between the inclusion level of krill meal
931 within feed and the increase in attractability and feeding consumption of *L. vannamei* to that
932 feed in the first 60 minutes after the food was presented. However, detection of the chemical
933 does not necessarily imply that the diet will be acceptable or consumed and assimilated

934 efficiently; indeed the attractiveness of the diet may become attenuated with time (Lee &
935 Meyers 1997). It is also important that the level of attractant is not too high as desensitization
936 can occur (Pittet *et al*. 1996). Moreover, water quality can affect the crustacean's ability to
937 detect and respond to chemicals (Lee & Meyers 1996; Koehl 2006, 2011; De la Haye *et al*.
938 2012).
939
940 Even if an individual shrimp is attracted to a food source, there are numerous external and
941 internal influences which may alter its behaviour (see Fig. 1). Another area of behavioural
942 research that has been used to the benefit of aquaculture practice has focused on optimal
943 feeding strategies and how feed is presented. Although recently some countries have adopted
944 more complex feeding protocols (e.g. automatic feeders, acoustic feeding-control) (Bador *et*
945 *al*. 2013; Jory 2016), most feed management strategies have remained largely unaltered since
946 the mid-1980s (e.g. manual broadcasting) (Carvalho & Nunes 2006; Jory 2016). Feed is
947 commonly offered between two to four times per day with the ration based on shrimp
948 biomass and the eaten-uneaten feed ratio (Jory 1995; Pontes *et al*. 2008; Lima *et al*. 2009).
949 Feed is generally supplied to the shrimp in feeding trays which are a good tool for the
950 estimation of how much shrimp are eating daily and allow spatial feed distribution
951 throughout ponds (Bador 2000; Cuéllar-Anjel *et al*. 2010). Frequency of feeding may change
952 seasonally (Seiffert & Andreatta 2004) and distribution of the daily ration in different
953 percentages is common practice (Jory 1995). However, understanding how individuals
954 respond to different feed presentations will be important in maximising efficiencies.
955
956 Feed has to be consumed by shrimp in the first two hours after feed has been introduced into
957 the water, before changes in the physical and chemical characteristics of the pellets occur,
958 leading to a reduction in feed attractant properties and nutrients which leach into the water

(Sick *et al*. 1973, Smith *et al*. 2002; Carvalho & Nunes 2006; Cuéllar-Anjel *et al*. 2010). Water absorption also makes the pellets more difficult for shrimp to manipulate into their buccal cavity (Sick *et al*. 1973). While *P. monodon* has been observed to consume pellets from feeding trays which had been in the water for up to 4 hours (Smith *et al*. 2002), uneaten food crumbles, and is consequently not consumed (Martinez-Cordova *et al*. 1998), leading to deterioration in water quality (Nunes *et al*. 1996; Sanchez *et al*. 2005). Ensuring that food is provided at the most appropriate times and rations is, therefore, important. In some studies, an increased feeding frequency has had a positive effect on shrimp growth (Robertson *et al*. 1993; Wyban *et al*. 1995; Tacon *et al*. 2002) whereas other studies have found no direct relationship between these two factors (Velasco *et al*. 1999; Smith *et al*. 2002; Carvalho & Nunes 2006). Greater behavioural exploration levels, feed conversion ratios and growth rates in *L. vannamei* resulted from three to four feedings per day (Pontes *et al*. 2008; Lima *et al*. 2009); however, feeding more than twice per day may not be desirable for aquaculture as it is labour-intensive (Carvalho & Nunes 2006). More than four feedings per day could also elicit a loss of stimulation to the shrimp and reduce overall feeding. As previously mentioned, automatic feeders are being implemented more frequently in *L. vannamei* aquaculture (e.g. AQ1 systems). Jescovitch *et al*. (2018), testing different feeding protocols, determined that automatic feeders produced the best results in terms of pond biomass of shrimp. However, they also resulted in the highest levels of nitrogenous compounds. This technology does however present a large potential application for shrimp farming, but its use must be properly adjusted to shrimp feeding activity, an area where behavioural studies could provide useful information.

A full analysis of daily behavioural feeding patterns can help refine feeding practices (Lima *et al*. 2009). Verifying the time of the day when shrimp are most likely to perform searching

behaviours allows feed provision at a time when shrimp are most likely to eat it (Da Costa *et al.* 2016). For example, introduction of feed elicited feeding behaviour arousal and exploration in *L. vannamei* within 30 minutes, with the most efficient feeding rates occurring in the morning and afternoon compared to the night (Pontes & Arruda 2005a). Although *L. vannamei* individuals were more active during the night, this was not influenced by the presence of food. Pontes *et al*. (2006) showed feeding *L. vannamei* once a day at random times resulted in substrate exploration in both light and dark phases, suggesting that the search for food occurs both during the day and night. Studies with other shrimp species, such as the Southern brown shrimp (*Penaeus subtilis* Pérez Farfante), have found the greatest feeding activity 10 minutes after onset (Nunes *el al.* 1997) and that peaks in ingestion of natural food occurred around 30 minutes after the addition of artificial feed (Nunes *et al*. 1996). Taken together, these behavioural results suggest that feeding times spread out over the course of the day may stimulate search behaviours and lead to greater ingestion of feed and is why continuous feeding is now often used in shrimp farming. There are many other factors which may determine the success of food distribution, however, few have been studied in detail in shrimp aquaculture. In finfish aquaculture, distribution of food and feeding times is an important consideration, for example, in the formation of social hierarchies (Chandroo *et al*. 2004; Bégout *et al*. 2012; Martins *et al*. 2012), and similar behaviours may affect shrimp feeding.

1003 **Table 2.** Studies on the behaviour of shrimp in response to feeding effectors. Water quality parameters that shrimp were held under prior to and/or during behavioural
1004 observations are given, whether behaviours were observed in shrimp held individually or in groups and whether anything is known about the moult stage or sex. The
1005 presence of any substrate or environmental enrichment is noted. Feeding effectors listed are the most effective for that particular study.

Feeding Effectors (selection)	Inclusion level (%)	Base Feed	Species	Behaviours Measured	Water Quality Parameters	Juveniles/Adults	Moult Stage	Single (S) or Group (G)	Substrate or Environmental Enrichment	Reference
Taurine Yeast extract	1.5	Control diet (using 1.5% α-cellulose in place of an attractant)	*Penaeus monodon*	Diets in paired choice	29±1°C, 25 ppt, 12:12 h	Juveniles	-	G, 8 shrimp	30% water exchange/day	Hartati & Briggs, 1993
Heat-dried squid Krill hydrolysate Fish hydrolysate	3, 9, 15	Commercial feed (35% CP)	*Litopenaeus vannamei*	None	28±0.5°C, 32 ppt	Juveniles	-	G, 8 shrimp	80% water exchange/day	Córdova-Murueta & García- Carreño, 2002
Krill meal	4	Wheat-flour-casein based feed (16% and 45% CP)	*Litopenaeus vannamei*	Feeding activity within feeding trays (predetermined time intervals)	28-29°C, 27.3-28.2 ppt, DO 5.8-6 mg/l, 12:12h	Adults	Same moult status	G, 50 shrimp	50% water exchange/day	Sanchez *et al*., 2005
Squid meal Crustacean meal Krill meal	1, 2.5, 5	Base feed (terrestrial source)	*Penaeus monodon*	Diets in paired choice using feeding trays	27±2°C, 12:12h	Juveniles	Inter-moult	G, 12 shrimp	-	Smith *et al*., 2005
Amino acid complex Whole squid protein hydrolysate Condensed fish soluble protein	0.5, 1, 3	Neutral gelatine pellets	*Litopenaeus vannamei*	Detection, orientation+ locomotion and feeding activity with paired choice using Y-maze	33 ppt	Juveniles	-	S	-	Nunes *et al*., 2006

Dimethyl sulphide Trimethylamine oxide Trimethylamine	0.5, 0.01	Commercial feed	*Penaeus monodon*	Time spent to approach and pick up the feed	27±0.2°C, 30±2ppt, pH 8.0±1	Juveniles	-	G, 5 shrimp	-	Ahamad-Ali *et al*., 2007
Squid liver meal Krill meal	3	Poultry by-product meal at 20% + base feed (46% CP)	*Penaeus stylirostris*	Diets in paired comparisons (dietary choice)	28-31°C, 27-30 ppt, pH 7-8.2, DO > 5mg/l	Juveniles	-	G, 10 shrimp	-	Suresh *et al*., 2011
Krill meal	0, 1, 3, 6	Commercial feed	*Litopenaeus vannamei*	Consumption rate within 60 and 180 min	25-27°C, 32-35 ppt, 12:12 h	Juveniles	-	S G, 36 shrimp	-	Derby *et al*., 2016
Krill meal solution	0.00133, 0.0133, 0.133, 1.33, 13.3 mg/ml	Commercial feed	*Litopenaeus vannamei*	Specific behaviours measured such as 'Probe', 'Grab' in response to food.	25-27°C, 32-35 ppt, 12:12 h	Juveniles	-	S G, 36 shrimp	-	Derby *et al*., 2016

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CONCLUSIONS

Solutions to the problems associated with feed management and efficiency in crustaceans have been addressed by several nutritional and behavioural studies in crustacean aquaculture. However, what is clear from this work is it is vital that nutritional and behavioural studies are developed together to understand, for example, how the study of chemical components is important in enhancing feeding behaviours, such as arousal, search initiation and food location (Derby *et al*. 2016). Considering these types of studies in combination may also useful for improving palatability of commercial feeds and enhancing ingestion (Holland & Borski 1993; Lee & Meyers 1996; Samocha *et al*. 2004a; Sanchez *et al*. 2005; Smith *et al*. 2005; Suresh *et al*. 2011).

Very little work has thoroughly examined the sequence of feeding behaviour patterns, which can only be achieved through continuous behavioural monitoring linked to different feeding phases. In *L. vannamei*, nutritional studies have shown how different strategies, such as changing culture parameters (e.g. Rosas *et al*. 2001; Zhang *et al*. 2006; Bett & Vinatea 2009; Ponce-Palafox *et al*. 2013) or testing novel additives (e.g. Córdova-Murueta & García-Carreño 2002; Sanchez *et al*. 2005; Nunes *et al*. 2006; Derby *et al*. 2016), can help solve problems associated with feeding efficiency in the species. However, these studies are mainly focused on outputs such as survival or growth rate, with very few studies obtaining data on feeding behaviour patterns (e.g. Pontes & Arruda 2005a,b; Nunes *et al*. 2006). In addition, work is often carried out under laboratory conditions which then require scaling up to realistic farming conditions (Tacon 1996). There is also a need to focus research at the species level as many of the influences on shrimp behaviour will be species-specific. The majority of studies to date have not controlled for, or at least not reported, individual

variation in behavioural response, thus these influences are largely unaccounted for in our understanding.

Behavioural research in finfish aquaculture is extensive (e.g. Chandroo *et al*. 2004; Dingemanse *et al*. 2009; Bégout *et al*. 2012; Martins *et al*. 2012; Ibarra-Zatarain *et al*. 2016), and while driven primarily by welfare considerations, has led to significant refinements in feeding practice and efficiency. Recent reviews highlight the importance of applied behaviour in finfish aquaculture. For example, Zhou *et al*. (2017) defended the use of technological feeding control devices using behavioural research. Castanheira *et al*. (2017) highlighted the importance of coping styles in finfish aquaculture, and the idea that proactive (i.e. bold) and reactive (i.e. shy) fish have different fundamental requirements. Selection or accommodation of desirable traits can, therefore, increase growth and reduce aggression within an aquaculture environment. Our understanding of personality and associated behavioural traits in crustaceans is extensive, yet the literature is lacking a focus towards species in aquaculture. Thus, a large potential exists to improve feeding efficiencies in shrimp aquaculture with focused research on shrimp behaviour.

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